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THE COURSE OF THE BLOOD FLOW IN LUMBRICUS.[1]

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ALTHOUGH this form is almost universally used as a type for laboratory study, its circulation is still very imperfectly understood. The present contribution aims to give a better understanding of the course taken by the blood, as determined by observation and experiment upon large specimens of *Lumbricus terrestris*. The following brief review of the anatomy of the circulatory system, which is well understood, will serve as a basis for the discussion of the blood flow.

A large *dorsal vessel* extends along the dorsal surface of the intestine from the caudal end of the worm to the pharynx, over which it ramifies. Strong pulsations of this vessel run in more or less regular succession from the posterior to the anterior end. In somites VII to XI, inclusive, five pairs of circular vessels, the strongly pulsating *hearts*, encircle the œsophagus, connecting the dorsal vessel with the *ventral*. The ventral is a longitudinal trunk lying beneath the intestine and giving branches to the body wall and the nephridia. A *subneural* and two *lateral neural* vessels constitute, by reason of an irregular network of anastomoses between them, a connected system accompanying the nerve cord. This system is connected through branches of the lateral neurals with the body wall.

Connecting the dorsal and subneural vessels are the so-called *parietals*. They occur, one pair in each segment beginning with XII, close behind the septa and give off branches to the body wall and the nephridia. The parietal in somite XII is much larger than the others. In each somite two or more unpaired *ventro-intestinal* vessels enter the wall of the intestine from the ventral vessel, while two pairs of *dorso-intestinals* pass from the dorsal vessel into the wall of the intestine.

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[1] From the Zoölogical Laboratory of West Virginia University.

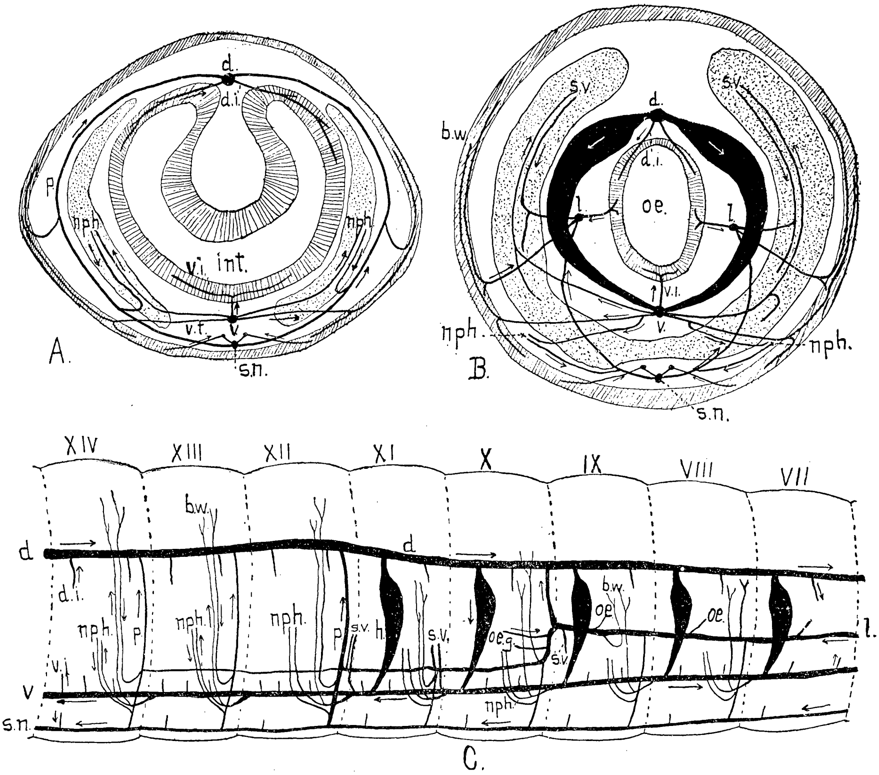
In somite X a pair of *lateral* vessels come from the dorsal vessel and run forward on either side of the œsophagus to the pharynx, giving branches to the œsophagus and body wall. An anastomosing vessel arises from the lateral near its origin in somite X and passes backward to join the large parietal in somite XII. From this anastomosis, branches supply the seminal vesicles, which are also supplied from the ventral vessel. Connecting vessels between the laterals and subneurals occur in several somites.

The only points with regard to the course of the blood flow upon which authors agree are that the blood flows forward in the dorsal vessel to the hearts, downward in the hearts, and backward in the ventral vessel. With regard to the further course of the blood Perrier came to the following conclusions (as reported by Bourne and Harrington): the blood flows into the dorsal vessel from the parietals and from it through the dorso-intestinals; the ventro-intestinals carry blood from the intestine to the ventral vessel; from the ventral it is given to the body wall and nephridia and is gathered up from these by branches from the lateral neurals and parietals; the flow in the laterals is forward.

Bourne ('91) studied the blood flow in Megascolex principally by holding the vessels with forceps and by cutting them to see from which cut end the blood flowed. His conclusions are nearly opposite to those of Perrier, namely, that the dorso-intestinals empty into the dorsal and the parietals carry blood away from it; the ventral gives blood to the intestine through the ventro-intestinals; it also gives blood to the body wall and nephridia, from which it is carried to the intestine (in Megascolex) by the intestino-tegumentaries. The lateral vessels carry blood backward.

Benham ('91), working on Lumbricus, agrees with Perrier in regard to the blood flow in all vessels.

Harrington ('99) has given a full account of the anatomy of the vascular system, with elaborate figures. His descriptions and figures, however, do not always agree, *e.g.*, the common vessel branching into ventro-tegumentary and ventro-intestinal described on page 142 is not shown in the figures. Harrington



DIAGRAMS TO ILLUSTRATE THE SCHEME OF CIRCULATION GIVEN IN THIS PAPER.

A, cross section of body region; *B*, cross section through hearts; *C*, sketch of vessels in somites VII to XIV seen from the side. Arrows indicate the direction of blood flow. *b.w.*, body wall and vessels supplying it; *d.*, dorsal vessel; *d.i.*, dorso-intestinals; *h.*, hearts; *int.*, intestine; *l.*, lateral vessel; *nph.*, nephridium and vessels supplying it; *œ.*, œsophagus and vessels supplying it; *œ.g.*, vessels supplying œsophageal glands; *p.*, parietals; *s.n.*, subneural; *s.v.*, seminal vesicles and vessels supplying them; *v.*, ventral vessel; *v.i.*, ventro-intestinals; *v.t.*, ventro-tegumentaries. The figures are unfortunately crowded, owing to the projection on one plane of many vessels which lie at different levels. The lateral neurals are not lettered in *A* and *B* and are not shown in *C*.

was the first to describe the arrangement of vessels to the integument, showing that the capillaries of the parietals ("commissurals") are directly continuous with those of the ventro-tegumentaries, and that loops of these capillaries lying just beneath the cuticle have the function of respiration. He has shown also that in somites VIII to XIII inclusive the subneural has a branch which supplies the nephridium and setigerous glands and anastomoses with the lateral. The lateral has connections with the dorsal in X and XII, as above described. Anastomosing vessels continue backward through XIII and XIV, making connections with the subneurals at each septum. These points have been verified by the present writers, but Harrington's statement that the true parietals ("commissurals") are absent in XIV and XV they cannot confirm. True parietals are always found in all somites back of XII, and occasional worms clearly show anastomosing vessels continuing backward from the laterals, connecting with the parietals of one or two somites. The anastomoses between the laterals and subneural have not always been found by the present writers in all the somites mentioned.

Harrington studied the course of blood flow by watching the pulsations of the vessels in small specimens of Lumbricus under a dissecting lens. He concludes that the blood flows forward in the dorsal, downward in the hearts, backward in the ventral, into the dorsal from the dorso-intestinals and out from it into the parietals ("commissurals"), forward in the laterals, and either forward or backward in the subneural.

The senior author has made observations on the course of the blood flow in connection with class work for a number of years. During this time the direction of flow in the subneural has been demonstrated in many student dissections, the result constantly agreeing with that stated below. The observations reported here have been made on the largest worms obtainable, anæsthetized and opened under physiological salt solution. The course of the flow in each vessel has been determined by the three methods of clamping, cutting the vessel, and watching the pulsations where these are visible. Injecting the dorsal vessel was tried several times, but as yet no facts regarding the course of the flow have been made out by this means, although the injection gives a good demonstration of the anatomy of the vascular system.

Description of Experiments.

Many experiments give no definite results, owing to the condition of the worm or to violent disturbance of the circulation. Great care is required in recognizing and interpreting the results, especially in observing pulsations. It has been found that when fairly clear and definite results are obtained, the same result is given by the different methods.

1. *The Dorsal Vessel.* — The fact that the blood flows forward in the dorsal vessel up to the hearts is clearly shown by the course of the pulsations. In front of the hearts the pulsations are not conspicuous, and special attention was given to determining the course of flow in this part of the dorsal. Among the many worms dissected a few were found in which the pulsations of the dorsal were distinctly seen running forward to the pharynx. The dorsal vessel was clamped in front of the hearts in a number of worms, and in all cases the blood collected behind the clamp and disappeared in front of it. The blood flows forward throughout the whole length of the dorsal.

2. *The Ventral Vessel.* — The experiments noted below and the general agreement of authors make it certain that the blood flows backward in the ventral vessel back of the hearts. The course of the flow in front of the hearts was shown by clamping the ventral vessel in the seventh somite. In every case the blood collected behind the clamp and disappeared in front of it, indicating a forward flow.

3. *The Subneural and Lateral Neurals.* — The best results are obtained on these vessels by opening the worms from the ventral side. When the subneural vessel was cut the blood flowed only from the anterior cut end, *i.e.*, backward. The same result was obtained constantly by pinching the subneural with forceps: the blood collected very distinctly in front of the forceps and disappeared behind them. These experiments were tried in all regions of the worm.

4. *The Parietals.* — Clamping these vessels has given doubtful results. The first experiments were made by pinching them at about the middle of their length in a number of worms. The blood seemed to collect between the dorsal vessel and the forceps. More recently no results whatever have been obtained from the parietal vessels by this method. This is perhaps due to the fact that branches from the body wall enter the parietals both above and below the forceps. In each of eight worms a dozen or more parietal vessels were cut, and in every case in which bleeding occurred the blood flowed from the lower end, that is, toward the dorsal vessel.

Owing to the numerous connections of the parietal vessels, it is necessary to use indirect methods to determine the course of blood flow in them. In several sets of experiments the attempt was made to determine the source of supply to the parietals and their place of emptying, by clamping or cutting other vessels. All three longitudinal trunks, dorsal, ventral, and neural, were simultaneously clamped, with the following results in each case. The dorsal vessel was filled on both sides of the clamp. Although the pulsations were sometimes seriously interfered with, its normal fullness was maintained. This is to be explained, as will appear from what follows, by the fact that in front of the clamps a complete circulation is kept up and the fullness of the dorsal maintained by the dorso-intestinals and parietals *both* emptying into it. On the theory that the parietals and dorso-intestinals carry blood in opposite directions, it must be expected that the dorsal would be empty in front of the clamp in this experiment. If only one set of circular vessels empty into the dorsal, its own pulsations together with the other circular vessels must certainly drain it of blood in front of a clamp. Behind the clamp it is to be expected that the dorsal should be full, but the normal fullness is not greatly exceeded, because the clamping of the ventral and neurals cuts off the supply of blood to the posterior end of the worm. It is also possible that the course of flow is reversed in the parietals or dorso-intestinals or both, just behind a clamp on the dorsal, because of the excessive pressure developed by the pulsations of the latter vessel. In this experiment the ventral and neural vessels were filled in front of, and empty behind, the clamps, indicating a backward flow in both. The parietals were filled both in front and behind the clamp. They were somewhat distended in front of the clamps, owing to increased pressure from the subneural in front of its clamp, while behind the clamps the parietals continued to collect some blood from the body wall and nephridia.

In four worms the ventro-intestinals in several segments were cut in order to drain the intestine of blood in those segments, and the dorsal was afterward clamped at both ends of the area in which the ventro-intestinals were cut. Between the clamps the dorsal decreased and the parietals were normally full. In four other worms the same result was reached when the dorsal was clamped in one place and the dorso-intestinals were cut for several segments in front of the clamp. Since the dorsal retained some blood and the parietals kept up their normal fullness as long as the worm lived, while all other supply to the dorsal was cut off, it is impossible to reach any other conclusion from these experiments than that the parietals bring blood to the dorsal.

Pulsations of the parietal vessels are not always clearly visible. In four worms in which the pulsations of the parietals were distinct and strong a large number of these vessels were carefully studied. The contraction of the parietals occurs opposite the front part of the pulse wave of the dorsal, *i.e.*, while the dorsal is reaching its greatest fullness. The parietals fill just after the contraction of the dorsal, *i.e.*, opposite the point of constriction of the dorsal behind the pulse wave. The filling of the parietals is sudden and the contraction slow. This, taken together with the order of the contractions, indicates that the contraction of the parietals helps to swell the dorsal just in front of the constriction which carries its pulse wave along, while the rapid filling of the parietals is due to the sudden closure of the parieto-dorsal openings by the contraction wave of the dorsal. The results of all the experiments considered together strongly favor the conclusion that the parietals carry blood to the dorsal.

5. *The Dorso-Intestinals.* — When one clamp was put on the dorsal vessel and a number of parietals were cut just in front of it, the dorsal vessel only partly emptied; but when the dorso-intestinals in the same segments were cut the dorsal vessel emptied entirely. This and the experiments on the parietals described above, in which the cutting of the ventro-intestinals in one case and of the dorso-intestinals in another resulted in the decrease of the dorsal vessel in those segments, show that the dorso-intestinals carry blood to the dorsal.

6. *The Lateral Vessels.* — When the laterals are clamped either at both their connections with the dorsal in somites X and XII or in front of the connection in X, they remain full of blood, sometimes much distended, in front of the clamps. No vessels have given more positive and unmistakable results than these.

CRITICISM AND CONCLUSIONS.

There is no difference of opinion in regard to the blood flow in any part of the dorsal vessel. All authors agree that it flows forward to the extreme anterior end of the worm.

Bourne alone suggests that the blood flows forward from the hearts in the ventral vessel, since he considers that the strong contractions of the hearts would force blood forward as well as backward. Our experiments have confirmed this plausible view, and it may be regarded as proved that the blood flows forward in this part of the ventral.

Although previous workers have not agreed upon the functions of the parietals and dorso-intestinals, they all agree in assigning to these vessels opposite functions. The above experiments on the parietals, although not wholly decisive, give strong support to a different conclusion, namely, that both parietals and dorso-intestinals carry blood to the dorsal.

It follows necessarily that the ventro-intestinals supply the intestine with blood, as Bourne and Harrington contend.

According to Harrington's interpretation all of the blood in circulation would have to pass through the ventro-intestinals; in other words, all of the blood which is carried forward by the dorsal and all that which passes downward from the dorsal in each somite through the parietals must be carried to the dorsal by the ventro- and dorso-intestinals. It does not seem possible for all of the blood to take this course, owing to the small size of the intestinal vessels. It has been impossible for the present writers to arrive at a definite conception of the blood flow according to Harrington's scheme. He represents the blood as flowing in different directions in different parts of the same vessel, and as changing its direction in the same vessel from time to time. Our experiments give no confirmation whatever to either of these conclusions, except that the direction is permanently reversed in the front end of the ventral vessel and in the dorso-intestinals in front of the hearts as above described. Temporary reversal of the flow in limited regions might easily occur as a result of the animal's movements, and such phenomena may have led Harrington to erroneous conclusions, since he worked only by studying the pulsations through the skin with a hand lens. His scheme of the circulation is full of inconsistencies, due either to an attempt to avoid overloading small vessels and consequent breakdown of the scheme, or to the incomplete study of several genera, resulting in a patchwork which is not true for Lumbricus at least. It is but proper to say that these inconsistencies might have been removed had the author lived to see his work through the press.

Bourne states that the lateral vessels carry blood backward, Harrington that they carry it forward. Our results positively support Bourne's view and, together with the results on the parietals, suggest a new interpretation of the morphology of the lateral vessels. Bourne considers them to be the subneural ends of the parietals in this region, *but assigns to them an opposite function.* The following facts seem to show that the lateral vessels are formed by anastomoses between successive parietals, which carry the blood from the head region to the dorsal in somites X and XII, and that the lateral system therefore represents the parietals in the head.

1. Absence of true parietals in front of somite XII.

2. Connections of the laterals with the subneural in several somites (VIII–XIII) which correspond perfectly to the ventral

ends of parietals, having branches to the nephridia as the parietals do.

3. Connections of the laterals with the dorsal in somites X and XII, corresponding to the dorsal ends of parietals.

4. Anastomoses between the parietals of somites XII, XIII, and XIV, in apparent continuation of the laterals.

5. Presence of branches of laterals to the body wall along the septa, corresponding to respiratory branches of the parietals.

6. Presence of branches to the seminal vesicles, which are also supplied by branches from the ventral. Here, as elsewhere, branches of the parietals take up blood which is brought from the ventral. The parietals are in the best position to supply the vesicles which are developed from the septa.

The origin of the hearts and laterals and the position of the laterals within the circular hearts are problems which require more facts for their solution. An extended discussion of them is beyond the province of this paper, but one or two suggestions will be made. The suggestion of Harrington that the hearts are modified parietals is negatived by the presence of both parietals and hearts in somite X, and by the different ventral connections of the parietals and hearts. It seems more probable that the hearts are enlarged circular intestinal vessels, serving to carry the blood brought forward by the dorsal. The lateral vessels must have arisen as anastomoses between successive parietals serving to return the blood from the head (brought forward by both dorsal and ventral), to the dorsal behind the hearts. The dorsal connections of the parietals in front of the hearts have disappeared from disuse. The position of these anastomoses within the circular hearts seems to indicate that they, too, have been derived from the capillaries of the œsophageal wall, although later than the hearts. This suggestion would explain the branches of the lateral vessels to the œsophagus and hearts, which otherwise are unexplained.

Conclusions. — The course of the circulation in each segment behind the hearts is as follows: the branches of the lateral neurals and parietals collect blood from the body wall; the parietals take blood to the dorsal from the subneural, body wall, and nephridia; the dorso-intestinals give blood to the dorsal from the intestine; all of this blood goes forward in the dorsal to the hearts; through them nearly all of it is given to the ventral vessel, which sends it to the intestine through the ventro-intestinals and to the body wall through the ventro-tegumentaries.

The head region is supplied with blood by the dorsal and ventral vessels, and the neurals and laterals carry blood from it.

The dorsal and ventral vessels carry mixed blood, the dorsal receiving oxygenated blood from the parietals and non-oxygenated from the dorso-intestinals. The neurals carry oxygenated blood only. The dorsal and ventral vessels carry mixed blood to the head region; the laterals carry backward mixed blood, and the neurals oxygenated blood.

There is no support given by our experiments to the idea of a more or less complete segmental circulation in Lumbricus. The circulation is strictly systematic, the blood making a complete circuit from the hearts backward through a greater or less number of somites, upward through the body wall, nephridia, or intestinal wall, to the dorsal, and thence forward to the hearts. This scheme of circulation is simple, and the slight modifications of it, which occur in the head region only, have received at least an attempt at explanation above. The interesting and highly important question presents itself: What happens when a worm's head is cut off and it lives and regenerates a new head, or perchance a tail? With the removal of the hearts some substitute must be provided to carry the blood from the dorsal to the ventral vessel. A series of regeneration experiments have been begun to find the answer to this question.

October 23, 1901.

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